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The effects of repeated cutting on coppice response of *Terminalia sericea*

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Abstract
Key message **Although exposure to multiple cutting cycles reduces stored reserves, shoot diameter and shoot length, it, however, increases shoot production per resprouting stump and foliar nitrogen.**
Abstract In disturbance-prone environments with fluctuating seasonal rainfall such as savannas, the repeated cutting of the same trees eventually results in a possible decline in tree abundance. The effects of subjecting *Terminalia sericea* trees to one, two and multiple (eight) cutting events over a period of 2 years on coppice response were investigated in a savanna woodland in South Africa. Resprout shoot diameter, shoot length and the total cumulative diameter were lower in trees exposed to a high number of cutting events compared to trees exposed to one cutting event. Increasing the number of cutting events significantly reduced stem total non-structural carbohydrate levels in trees indicating a depletion of stored reserves. Foliar carbon content remained largely the same, while leaf nitrogen and phosphorus concentrations significantly increased with each cutting event, relative to uncut trees. Results indicate that trees cut once had not replenished depleted carbohydrate reserves even after a period of 18 months during which no cutting took place. Sustainable utilization of this tree species must allow for at least more than 18 months of undisturbed growth between harvests to allow for the replenishing of reserves.

Keywords Repeated cutting · Coppice response · Stored reserves · Total non-structural carbohydrates · Depleted · Replenishment

Introduction

There is much concern about the sustainability of intensive cutting of trees for firewood in communal rangelands in Africa (Twine et al. 2003; Kaschula et al. 2005a; Neke et al. 2006; Shackelton et al. 2004). Cumulative over-harvesting in these areas has contributed to degraded woodlands and thus diminished the availability of wood as a source of energy. Intensive cutting of trees severely depletes stored carbon reserves and potentially reduces growth. The process of replenishing stored carbohydrate reserves is largely dependent on trees striking the balance in being able to photosynthesize efficiently, grow sufficiently and then being able to have excess carbon for storage; all of this being dependent on soil moisture content and nutrient status (Cruz et al. 2003). However, little is known about the factors that control the reserve content of a plant, how much of the reserve is utilized after a disturbance such as a harvest (Cruz et al. 2003), and the changes in the recovery of nutrients such as nitrogen and carbon lost during a disturbance. These factors have significant implications for the sustainable use of rangelands subjected to intensive wood harvesting.

In systems prone to disturbances, such as savannas, the ability of savanna tree species to coppice is a key attribute of their resilience and productivity (Shackleton 2001;

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Kaschula et al. 2005b) because coppice growth is tolerant of drought and nutrient-poor soils (Kennedy 1998; Kaschula et al. 2005b). However, the ability of a woody plant to coppice and remain vigorous largely depends on the severity of the disturbance with reference to above ground biomass, availability of water and nutrients, and also on the availability and mobilization of resources above and below-ground (Nzunda et al. 2008).

Although resprouting has become recognized as a key functional trait in plant ecology over the past decade (Lawes and Clarke 2011), there is still limited information about the physiology and growth strategies of resprouting trees in savannas (Neke 2004; Pote et al. 2006). Available information about the influence of disturbance and cutting frequency comes from ecosystems that are different when compared with savannas. Coppicing is generally the primary regeneration mechanism after a woody plant has been cut or severely damaged, where stem and roots remain in place (Forrester et al. 2003). As a management tool, it has been proposed as a method for minimizing damage to indigenous vegetation through sustainable fuelwood production (Kennedy 1998). This is because coppice shoots grow faster than seedlings and they exhibit apical dominance, producing woody material for homestead utilization (Kennedy 1998; Hardesty 1987). The resprouting ability of a plant can have major impacts on tree recovery and re-establishment to reduce ecosystem dependence on seed production and germination for population maintenance and growth, because seedling establishment is not a reliable means of re-establishment, especially where resources such as water are limited (Bond and Midgley 2001).

The effect of continued shoot removal on total non-structural carbohydrates and regrowth of trees is poorly understood (Carpenter et al. 2008; Luostarinen and Kauppi 2005), especially in semi-arid, nutrient-poor rangeland ecosystems. In addition, the role of carbohydrate reserves in regrowth of intensively harvested woody species remains unclear, and therefore merits attention considering that some studies have suggested that trees mobilize stored nitrogen for use in regrowth instead of stored carbohydrates (Druege et al. 2000; El Omari et al. 2003; Wendler et al. 1995; Millard and Proe 1992). Since the availability of stored reserves is central to the vegetative regeneration after a cutting event, trees will respond through allocating resources to growth or defence strategies (Rooke and Bergstrom 2007). This allocation of resources is determined by various factors which include the availability of water, nutrients and sunlight during and after the disturbance, and the severity of damage on the plant caused by the disturbance (Katjiua and Ward 2006).

For plants, it is a biological advantage to have a readily available source of energy after a disturbance (Fornara and Du Toit 2007). This is because vegetative parts need to be maintained to initiate establishment of new photosynthetic surfaces for shoot recovery (Bowen and Pate 1993; Luostarinen and Kauppi 2005; Kozlowski 2002). Some woody plants store enough carbohydrate reserves in stumps and roots to meet more than one resprouting event following a disturbance (Carpenter et al. 2008; Luostarinen and Kauppi 2005). To recover after a browsing event which removes leaf material, a plant needs viable meristems and carbon reserves, at least until new shoots become functional and can photosynthesize (Kabeya and Sakai 2005). Resprouting trees also rely on stored carbohydrate reserves to support growth and respiration until sufficient leaf area has been regrown for carbon assimilation to meet growth demands (Chapin et al. 1990; Bond and Midgley 2001).

When photosynthetically efficient, a resprouting plant can reach peak growth and then allocate carbon towards storage (Kabeya and Sakai 2005). For example, Van der Heyden and Stock (1996) showed that after branch cutting, regrowth of the shrub *Osteospermum sinuatum* Norl. was dependent on stored carbon and this reliance shifted to photosynthates produced by new and remaining leaves. Canadell and Lopez-Soria (1998) also demonstrated that a large amount of total non-structural carbohydrates are mobilized when *Erica arborea* L. and *Arbutus unedo* L. were exposed to multiple clipping events. Bowen and Pate (1993) found that production of *Stirlingia latifolia* R. Br. decreased due to successive harvests, with root starch reserves higher for plants that were burnt once and allowed to recover compared to trees that were burnt and clipped. Shoot production was lower in frequently cut *Gliricidia sepium* (Jacq) compared to less frequently cut trees (Erdmann et al. 1993). Also, repeated clipping of the *Eucalyptus kochii* Maiden resulted in eventual death of the tree, with TNC reserves shown to be higher for trees not cut compared to trees recovering from a single cut (Wildy and Pate 2002).

The objective of this study was to investigate how repeated cutting of trees affects their ability to regenerate and also how the concentration of stem-stored reserves changes, as well as foliar carbon (C), nitrogen (N) and phosphorus (P). It was hypothesized that repeated cutting negatively affected resprouting after a 2 year cutting period, while also significantly reducing stem total non-structural carbohydrates and increasing foliar N and P but with no effects on foliar C.

Methods

Study site

The study was conducted at the Wits Rural Facility (WRF), a 350-ha research station owned by the University of the

Witwatersrand, in the central savanna lowveld ecoregion of Limpopo Province, South Africa (24°30′S; 31°06′E). The study site is semi-arid, with a mean annual precipitation (MAP) of ~650 mm, concentrated in the summer season (between October and April) (Kaschula et al. 2005a; Shackleton 1997; Neke et al. 2006). The study spanned a 2-year period (Sept 2010–Sept 2012), starting at the end of the dry season of 2010, during the period when trees begin leaf-flush. Rainfall totals over the study period were above-average (825 and 915 mm in years 1 and 2, respectively). The mean annual temperature is 22 °C (Neke et al. 2006; Shackleton 1993). Drought events are common and occur about every 4 years (Neke 2004). The most common soil types in this region are the shallow, sandy, nutrient poor lithosols, underlain by granitic gneiss (Shackleton 2001; Neke et al. 2006; Kaschula et al. 2005a; 2005b). The vegetation is dominated by tree species in the Combretaceae (notably *Terminalia sericea*) as well as Mimosaceae (e.g. *Acacia gerrardii* Benth) families, characteristic of the Mixed Lowveld Bushveld vegetation type (Shackleton 2001; Neke et al. 2006; Shackleton 1993).

Study species

The species chosen for this study was *Terminalia sericea* Burch. ex. DC, also known locally as silver cluster leaf. It is a common tree species in dystrophic savannas occurring from Tanzania and the Democratic Republic of Congo, southwards to Angola, Namibia, Zimbabwe, Botswana and South Africa (Coates-Palgrave 2002). *T. sericea* is a medium sized semi-deciduous tree species, growing (when uncoppiced) as a single-stemmed tree reaching up to 8 m in height or a multi-stemmed shrub 4–6 m tall (Coates-Palgrave 2002).

T. sericea is particularly prolific on the mid-slope seeplines of these ecozones, where it grows in dense groups of various sizes forming thickets producing a very large biomass (Amri 2011). It is one of the most commonly used fuelwood species in many parts of southern Africa, and is also used for medicinal purposes such as curing diarrhoea, in rural communities (Carr 1994; Neke 2004). *T. sericea* was chosen as the study species because more knowledge of its regenerative capacity can contribute to management recommendations for sustainable utilization. This was also because of its high capacity for coppicing and its tendency to form thick stands (Shackleton 1993; Neke 2004; Shackleton et al. 2004).

Experimental procedure

A completely randomized experiment with three treatments replicated at three sites was established in September 2010, to determine the effects of repeated cutting on the coppice response of cut trees. Ten trees were selected per treatment plot, numbering a total of 90 trees for the experiment. Although there were differences in initial stump diameter, single-stump trees were selected based on initial tree stump diameter; which was standardized (from 5 to 9 cm) to control its effects on coppice response. In cases where single stump trees could not be used, multi-stump trees of a combined diameter ranging between 5 and 9 cm were used. Stumps of that diameter range were considered medium-sized and were chosen because it has been suggested that larger stumps take a shorter time to respond to a cutting event, positively influencing initial coppice growth through having a larger residual root system (Shackleton 1997).

Trees were exposed to three cutting regimes over a 2-year period, based on pilot studies and unpublished data on tree cutting intensities in the nearby communal lands. Treatments began in September 2010 to September 2012 as follows (Fig. 1)

1. Cut once over the 2 year period in September 2012, termed cutting regime **a** (CRa);
2. Cut twice over the 2 year period in September 2010 and in September 2012, cutting regime **b** (CRb), and
3. Cut in three-month cycles over the 2-year period beginning in September 2010 and ending in September 2012, resulting in eight successive cutting events, cutting regime **c** (CRc).

For the first cut under each regime, trees were cut at a height of approximately, 25 cm from the ground. Since research has shown that the production of resprouting shoots increases with cutting height (Shackleton 1997; Khan and Tripathi 1986; Ibrahima et al. 2007; Kaschula et al. 2005b), the height used in this study was kept constant to minimize its effects on resprouting. Successive harvests for CRb and CRc were done through removing all resprouting shoots from the stumps.

Morphology measurements

Monitoring of trees for morphological changes started at the end of October 2012 and ended at the end of February 2013 because trees in CRb were being used in other experiments. For each resprouting stump, the following variables were measured monthly: (1) total number of shoots resprouting, (2) number of leaves on the leader shoot, (3) shoot length on the leader shoot and (4) shoot diameter on the leader shoot. Shoot production was calculated as the number of shoots produced per unit area of stump which was calculated from the stump diameter, while total cumulative diameter (TCD) was calculated as the product of the diameter of each leader shoot and the total number of shoots produced per stump. The assumption was that the diameter measured on each of the leader

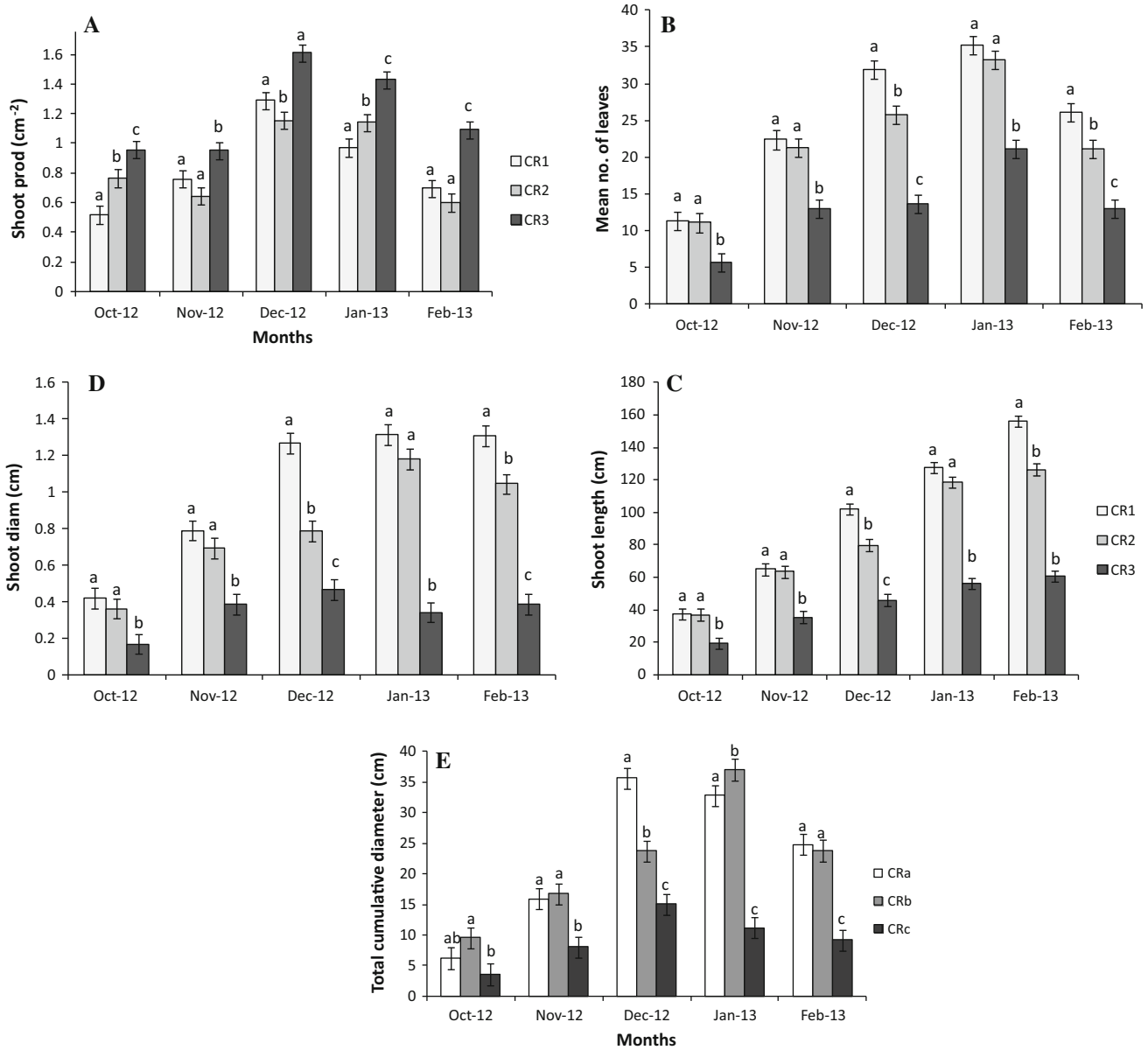

Fig. 1 The monthly effects of exposing *T. sericea* to different cutting regimes on **a** shoot production, **b** mean number of leaves, **c** resprout shoot diameter, **d** resprout shoot length and **e** total cumulative diameter from October 2012 to February 2013. Means within a month having different *small letters* (*a*, *b*, *c*) are significantly different at $p < 0.05$. Mean differences for mean number of leaves as indicated by the small letters (*a*, *b*, *c*) were compared using simple means comparisons. *CRa* cut once, *CRb* cut twice, *CRc* cut eight times. Means are represented with standard *error bars*

resprouting shoots was representative of the mean of all resprouting shoots per stump.

Above-ground storage analysis

Total non-structural carbohydrate reserves were determined for all experimental trees using wood cores, each of 3 cm long with a diameter of 4.3 mm. Since measurements were made before the end of the experiment, samples were collected from the uncut, trees cut once and trees cut seven times at the time of sampling. Two cores were extracted per tree stump (at 7 and 20 cm above soil level) using an increment borer, at the end of the growing season in April 2012. This means stem samples were collected when CRc trees had been cut seven times, CRb trees had been cut once and CRa trees had not been cut at the time of sample collection. Before storing the cores in airtight plastic bottles, the outer tree bark was immediately removed from cores after sampling. The core samples were then bottled and placed inside a freezer. Drying of samples was done at

65 °C for 2 days (assumed dry) and then samples ground using a coffee grinder before finer grinding through a 40 μm-mesh Wiley mill screen, at the University of Florida, USA. A composite sample was obtained after grinding. The TNC was determined on a dry weight basis using the anthrone method described by Edwards et al. (2011). The TNC values reported here are the sum of the soluble (glucose and sucrose) and insoluble (starch) fractions.

Foliar analysis

For C, N and P levels, leaf samples were collected from uncut trees and trees cut seven times at the end of the 18-month sampling period (end of March 2012). Trees from CRb were being used for another experiment at the time sampling and could not be used at that time. Leaves were collected a month after leaf flushing at the beginning of each growing season during the study (end of September 2010 and 2011), and in the middle of each growing season during the study (January 2011, 2012), when leaf production was assumed to be at its highest, and at the end of each growing season during the study (March 2011, 2012). Leaves were not collected in the dry seasons during the study because trees were shedding leaves during that period (i.e. between June and August). Leaves collected were oven-dried at 60 °C for 48 h and then ground using the Wiley mill. Leaf samples from a total of seven harvests (a period of 18 months) were taken to the University of Florida Laboratory for C, N and P concentration analyses. Total C and N were measured using a Costech ECS 4010 Elemental Analyzer (Valencia, CA, USA), while P was measured using the modified single solution method described by Murphy and Riley (1962).

Statistical analyses

The total number of shoots, shoot diameter and length data were log-transformed because data were not normally distributed, prior to analysis. No other data were log-transformed. For the response variables of number of shoots on resprouting trees and mean number of leaves on resprouting shoots a generalized linear mixed model (GLMM) was fitted by considering an underlied Poisson distribution with a logit link. The linear model included the fixed effects of cutting regime. In addition, random terms of site and tree within site were included. All models were fitted using the procedure GLIMMIX as implemented in SAS v. 9.2 (SAS Institute, Cary NC, USA). Significance of fixed effect terms were evaluated with an approximated F-test, and mean comparisons between regimes were obtained using least square means with Dunnett's T3. The simple means comparison (unprotected) was used to obtain the level of significance for the total number of shoots. The effects of repeatedly cutting *T. sericea* on coppice response (shoot diameter and length), total non-structural carbohydrates were analysed using analysis of variance, while the effects of cutting on C, N and P levels were analysed using the repeated measures analysis of variance. Dunnett's *T*3 test was used for mean comparison at $p < 0.05$ (Table 1).

Results

Effects on coppice response

The total number of shoots was significantly higher in CRc trees compared to CRa in October 2012, January and February 2013, while there were no significant differences in the total number of shoots due to treatment effects in December 2013 (Table 2). Exposing *T. sericea* to different cutting regimes had significant effects on the coppice response of resprouting trees. Shoot production was significantly higher in repeatedly cut trees (CRc) through-out the monitoring period compared to the other treatments

Table 1 The representation of treatments in the study in three sites showing the three treatments randomly allocated to each site

Site 1	Site 2	Site 3
Cut once (September 2012) (CRa)	Cut twice; (1) September 2010 (2) September 2012	Cut in 3 month cycles from September 2010 till September 2012
Cut in 3-month cycles from September 2010 till September 2012	Cut once (September 2012) (CRa)	Cut once (September 2012) (CRa)
Cut twice; (1) September 2010 (2) September 2012	Cut in 3 month cycles from September 2010 till September 2012	Cut twice; (1) September 2010 (2) September 2012

Table 2 The monthly effects of exposing *T. sericea* to different cutting regimes on the total number of shoots

	CRa	CRb	CRc
Total no. of shoots			
October	15 ± 4^{a}	27 ± 5^{b}	22 ± 5^{b}
November	20 ± 6^{a}	24 ± 5^{a}	23 ± 5^{a}
December	29 ± 6^{a}	30 ± 5^{a}	33 ± 4^{a}
January	25 ± 5^{a}	32 ± 5^{b}	33 ± 4^{b}
February	18 ± 3^{a}	22 ± 6^{b}	24 ± 4^{b}

Superscript letters compare treatment means within a month. Means with different letters (a, b) indicate significance across treatments (tested using simple means comparisons). Means are represented with the standard deviation

CRa cut once, *CRb* cut twice, *CRc* cut eight times

(Fig. 1a). In some instances, e.g. in November 2012 and February 2013, differences between trees cut once (CRa) and trees cut twice (CRb) in shoot production were not significant.

For the number of leaves produced, there were no significant differences between CRa and CRb trees in October 2012, November 2012 and January 2013, while CRa and CRb trees had significantly higher mean leaf numbers compared to CRc trees in December 2012 and February 2013 (Fig. 1b). Resprout shoot diameter and shoot length for CRa and CRb trees (Fig. 1c, d) were significantly higher than those for CRc trees throughout the study, while CRb trees recorded higher resprout shoot length and shoot diameter than CRc trees from November 2012 onwards. The TCD was significantly lower in CRc trees compared to the other treatments from November 2012 onwards (Fig. 1e).

Effects on total non-structural carbohydrates (TNC)

Exposing *T. sericea* to different cutting regimes had a significant effect on TNC levels, with levels declining significantly with an increase in the cutting frequency (Fig. 2). The TNC levels in trees cut seven times at the time of sampling were one-third that of uncut trees, while levels in trees cut once were half the levels in uncut trees.

Effects on Foliar C, N and P levels (%)

There was a significant cutting effect ($F = 42.97$; $p < 0.05$) of trees on foliar N levels (Fig. 3). Cutting trees from the period September 2010 to March 2012 (time effect) also had an overall positive significant effect ($F = 27.73$; $p < 0.05$) on foliar N levels of cut trees, while there was also a significant interaction between time (period of exposure to cutting treatments (September 2010–March 2012) and cutting effect ($F = 3.87$; $p < 0.05$) on N levels. There were no significant cutting effects ($F = 1.17$; $p > 0.05$) on foliar C levels. The period of exposure to cutting treatments also had no significant effect on C levels ($F = 0.42$; $p > 0.05$), and there was no significant interaction ($F = 2.49$; $p > 0.05$) between time and cutting effects on C levels (Fig. 3). There was a significant cutting effect ($F = 9.92$; $p < 0.05$) of trees on foliar P levels. The time effect also had a significant positive effect ($F = 6.85$; $p < 0.05$) on P levels, while there was also a significant interaction between the time effect and cutting effect ($F = 5.49$; $p < 0.05$) (Fig. 3).

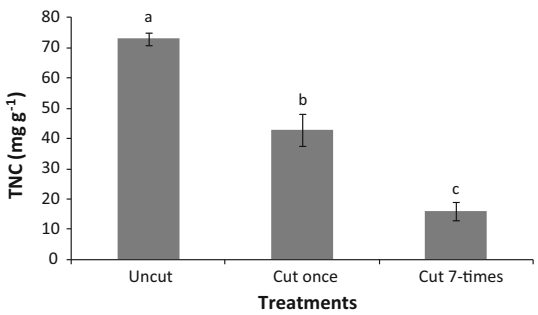

Fig. 2 Mean (dry weight) total non-structural carbohydrates (TNC) in three harvesting regimes in April 2012. *Bars* with different *small letters* (*a*, *b*, *c*) indicate significant differences at $p < 0.05$. Means are represented with standard *error bars*

Discussion

Effects on coppice response

The higher shoot production, but with fewer leaves for the repeatedly cut trees may have been a response to increase the surface area for photosynthesis, increasing carbon assimilation for use in either growth or replenishment of stem carbohydrate reserves. High shoot production in repeatedly cut trees may also have been a result of higher reserve mobilization late in the dry season and early into the growing season as suggested by Wildy and Pate (2002); Cruz and Moreno (2001). However, the relative decrease in the resprout shoot diameter in repeatedly cut trees was not off-set by the relative increase in the total number of shoots and also with the high shoot production in repeatedly cut trees not compensating for the disadvantage of the small size of the resprouting shoots.

Since stored TNC reserves are the most important source of carbon to support growth and recovery of a plant after a disturbance (Canadell and Lopez-Soria 1998; Chapin et al. 1990; Van der Heyden and Stock 1996), the similarities in the response of trees cut once and trees cut twice can be explained with reference to fluctuations in stored carbohydrate reserves. This is because trees cut twice were not cut until after a 2-year period, thus potentially allowing restoration of stored reserves mobilized after the first cut in 2010. Early growth of shoots is associated with the mobilization of previously accumulated reserves of either nutrients or starch (Latt et al. 2000; Garcia et al. 2001; Canadell and Lopez-Soria 1998).

Repeatedly cut trees had the lowest coppice response when considering the other response variables in this study other than shoot production mainly because insufficient time for TNC replenishment between successive cutting events was short as suggested by Latt et al. (2000). For this study, the 3-month period between the cutting events was probably not sufficiently long to allow for trees to regrow and establish new photosynthetic mass.

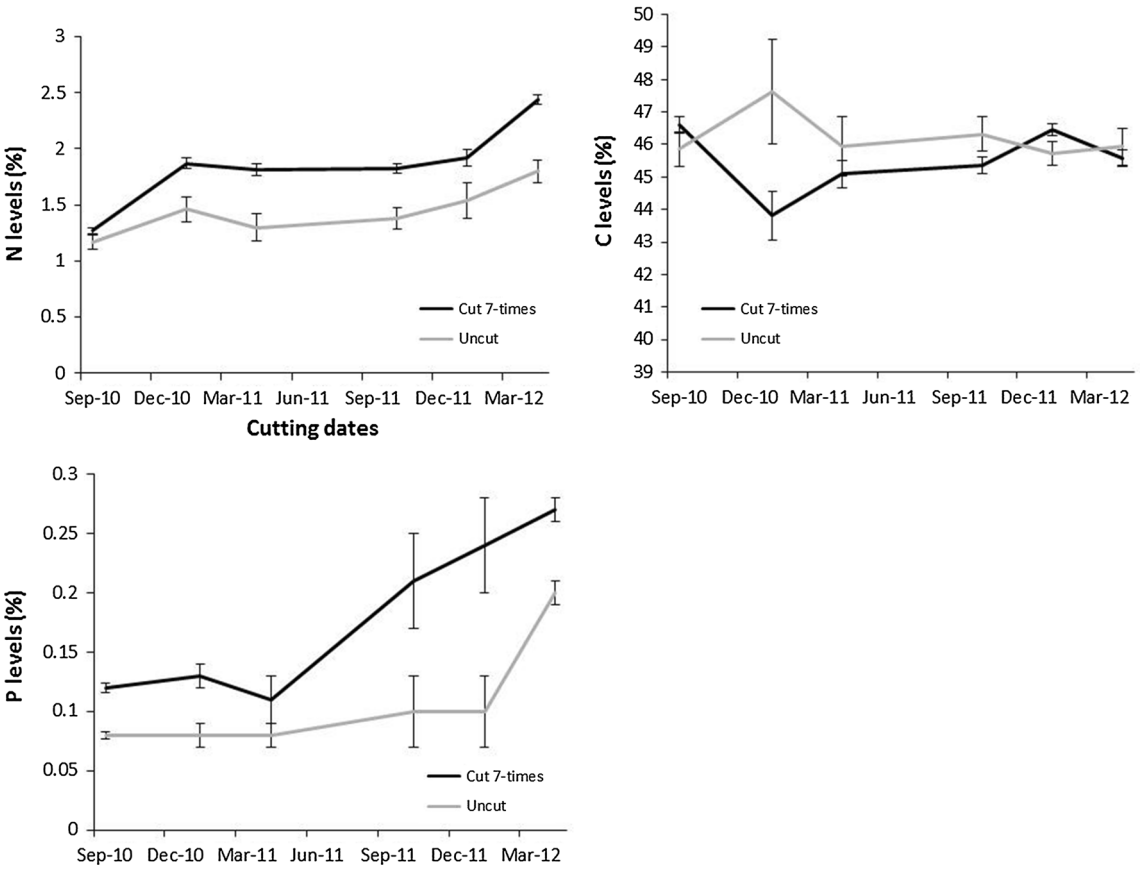

Fig. 3 Mean (%) nitrogen, carbon and phosphorus foliar concentrations of trees Cut 7-times and Uncut trees (from September 2010 to March 2012) (Cut 7-times represents trees from CRc, while Uncut represents CRa trees). Means are represented with standard *error bars*

Effects on stem TNC levels

After 18 months of recovery, trees cut once had not restored TNC levels to levels in uncut trees. The expectation was that after more than a year of regrowth, TNC levels would have reached those of uncut trees. Bowen and Pate (1993), proposed that TNC reserve levels initially decrease after a cutting event and that the reserve levels are expected to increase only after shoot biomass has reached similar levels to that before cutting. Trees cut once had significantly higher TNC levels compared to repeatedly cut trees because there was a regrowth period of more than a year, during which the trees had the opportunity to balance the TNC sink and source activity that was shifted after cutting.

The results imply that when trees are cut once, higher quantities of TNC reserves are mobilized for regrowth compared to when trees are cut seven times. Results from the study agree with other studies in which TNC reserves in woody plants have been shown to decrease as regrowth occurred after cutting, burning and defoliation (Miyanishi and Ellman 1986; Bowen and Pate 1993; Canadell and Lopez-Soria 1998; Landhausser and Lieffers 2002; Schutz et al. 2009; McPherson and Williams 1998; Luostarinen and Kauppi 2005). Concentrations of TNC were also highest in trees cut less frequently compared to trees harvested more frequently in *Gliricidia sepium* (Jacq.) (Garcia et al. 2001), in *Salix nigra* (Carpenter et al. 2008) and also in *Populus maximowiczii* (Henry) (Tschaplinski and Blake 1995).

Effects on Foliar properties

Subjecting trees to repeated cutting significantly increased leaf N compared to uncut trees, especially after 18 months. Leaf samples may have been of different ages, leading to younger leaves in repeatedly cut trees having higher N levels. The C:N ratio in trees cut seven times was 18 whereas in the uncut trees it was 33. This implies that the trees cut multiple times accumulated significantly more N in their tissue relative to C compared with trees which were uncut. This evidence points to the changed metabolic state of younger leaves in the multiple cut trees. Alternatively, an increase in leaf N can also be explained by increased investment in the production of leaf defences such as alkaloids (Eloff et al. 2008; Onoda et al. 2004) because

high levels of polyhydroxyalkaloids have been found in *T. sericea* (Eloff et al. 2008; Katjiua and Ward 2006).

Short-term responses to above ground branch removal in *Combretum apiculatum* Sonder showed that over the season, leaf N levels were higher on severely defoliated trees compared to trees not defoliated (Rooke and Bergstrom 2007). Leaf N levels were higher for *Cardiopetalum callophylum* (Annonaceae) and *Maprounea guianensis* (Euphorbiaceae) trees clipped monthly compared to trees clipped after every 3 months (Mundim et al. 2012). There were also higher leaf N levels on heavily browsed *Acacia nigrecsens*, Miller, compared to lightly browsed trees (Fornara and Du Toit 2007).

Since trees were sampled for TNC after seven events, it would be interesting to follow how the TNC levels change as the cutting cycles are increased to more than seven because it has been proposed that mortality in trees eventually occurs if the reserves are sufficiently depleted through trees being repeatedly clipped (Cruz et al. 2003; Miyanishi and Ellman 1986; Wildy and Pate 2002).

Implications

Repeatedly cut trees utilized TNC reserves after every cutting event, depleting stored reserves and contributing to reduced coppice response. Although cutting trees repeatedly may result in the highest number of resprouting shoots, this may not necessarily result in higher resprouting or regrowth rates because the diameter of the shoots do not compensate for the higher number of shoots produced to increase the resprouting response. The period between successive cutting events is critical for replenishing stored TNC reserves. To ensure sustainable utilization, this study indicates that trees require at least a minimum period of more than 3 months to replenish stored reserves. This would allow the recovery and replenishing of TNC reserves between successive cutting events and reduce the possibility of exhausting reserves, with the potential for ultimate mortality. It is proposed that a rotational period or recovery time of at least 6 months be used to allow trees to replenish part of the stored reserve mobilized after the initial harvest.

Authors contribution statement H. Moyo as the first author, designed the study, carried out the field work and data collection including the analysis and writing up of the paper. M. C. Scholes as the co-supervisor, assisted with guiding the first author and reading drafts of the paper. W. Twine- as the principal supervisor, read and corrected drafts of the paper as well as formulating the study design.

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Conflict of interest The authors declare that they have no conflict of interest.

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